

Pliocene vertebrate locality of Çalta, Ankara, Turkey. 12. Paleoecology, biogeography and biochronology

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ABSTRACT

Integrated studies on the Pliocene vertebrate locality of Çalta provided abundant data on the environment of the fauna, its biogeographic relationships and its age. The fauna is dominated by animals adapted to relatively dry and open environments with loose soil and some water points. The presence of short-limbed herbivores and of ochotonids might indicate a landscape with some relief nearby. The Çalta fauna is mainly composed of elements with European and some Asiatic affinities. African affinities of some taxa are doubtful. The time range of some mammalian groups is discussed, the Çalta locality is dated as early MN15 (late Ruscinian).

KEY WORDS

Mammals,
Pliocene,
Ruscinian,
Turkey,
paleoenvironment,
biogeography,
biochronology.

RÉSUMÉ

Le gisement de vertébrés pliocènes de Çalta, Ankara, Turquie. 12. Paléoécologie, biogéographie et biochronologie. Des recherches multidisciplinaires sur la faune de vertébrés et les sédiments de Çalta ont permis d'obtenir des résultats sur l'environnement, les affinités de la faune et son âge. Cette faune est dominée par des éléments vivant dans un milieu relativement sec et ouvert, avec cependant quelques points d'eau et un sol meuble. Quelques herbivores à pattes courtes et l'abondance des Ochotonidae suggèrent des reliefs dans le paysage. Dans cette faune, les groupes à affinités européennes sont plus nombreux que ceux à affinités asiatiques. Les rapports africains de quelques taxons sont sujet à caution. La synthèse des données biochronologiques permet de corréliser ce gisement à la partie inférieure de la zone MN15 (Ruscinien supérieur).

MOTS CLÉS

Mammifères,
Pliocène,
Ruscinien,
Turquie,
paléoenvironnement,
biogéographie,
biochronologie.

INTRODUCTION

In the present monograph on the Çalta vertebrate fauna, the sedimentology of deposits and the isotopic values of bones, teeth and soil samples are studied. Previous papers reported on amphibians, reptiles and some mammals, and also on the geological context of this locality. Therefore, a complete and reliable faunal list of Çalta is now available.

All these studies provide numerous data on environmental habits of various taxa and their biogeographic affinities. Moreover, the new criteria allow a better estimate of the age of this locality. Consequently, it is now possible to provide a synthetic view on the paleoecology of the site, the resemblances of the fauna with its equivalents from other regions, and to discuss its age.

FAUNAL LIST

The faunal list of the Çalta locality is as follows (the new taxa described from Çalta are indicated by an asterisk):

Gastropoda

Helix cincta Müller, 1781
Subzebrinus sp.

Amphibians

Pelobates sp.
Bufo sp. cf. *B. viridis* Laurenti, 1768
Rana sp.

Reptiles

Testudo sp.
Scincidae indet.
Lacertidae indet.
Ophisaurus sp.
Varanus marathonsensis Weithofer, 1888
Amphisbaenidae indet.
Scoleophidia indet.
Eryx sp.
Colubridae indet.
Palaeonaja sp.

Aves

Struthio sp.

Mammalia

Insectivora

Asoriculus gibberodon (Petenyi, 1864)
Mafia csarnotense Reumer, 1984
Soricidae indet.
Erinaceus sp.

Rodentia

**Centralomys magnus* (Sen, 1977)
Occitanomys sp.
**Orientalomys galaticus* (Sen, 1975)
Apodemus dominans Kretzoi, 1959
Mesocricetus sp. cf. *M. primitivus* de Bruijn et al., 1970
**Pseudomeriones tchaltaensis* Sen, 1977
Mimomys davakosi van de Weerd, 1979
Pliospalax macovei (Simionescu, 1930)
Dryomimus eliomyoides Kretzoi, 1959

Lagomorpha

**Ochotonoma anatolica* Sen, 1998

Carnivora

**Vulpes galaticus* Ginsburg, 1998

Nyctereutes donnezani (Depéret, 1890)

**Chasmaporthetes kani anatolicus* Ginsburg, 1998

Lynx issiodorensis (Croizet et Jobert, 1828)

Machairodus giganteus (Wagner, 1848)

Perissodactyla

Dicerorhinus megarhinus (de Christol, 1834)

**Hipparion heintzi* Eisenmann et Sondaar, 1998

Hipparion sp. cf. *H. longipes* Gromova, 1952

Artiodactyla

Sus arvernensis minor Depéret, 1890

Cervus sp. cf. *C. perrieri* Croizet et Jobert, 1828

Giraffa sp. cf. *G. jumae* Leakey, 1965

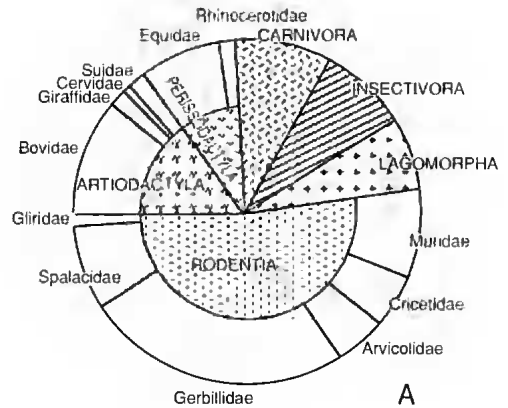
**Gazella emilii* Bouvraïn, 1998

**Tchaltacernus longicornis* Bouvraïn, 1998

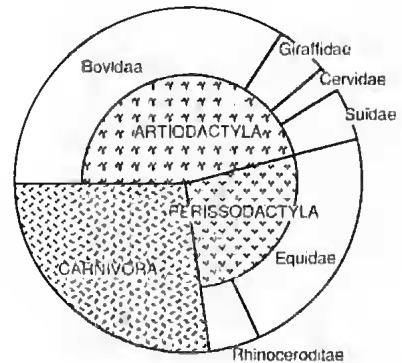
Bovidae indet. cf. *Koufotragus bailloudi* (Arambourg et Piveteau, 1929)

Gazellospira sp.

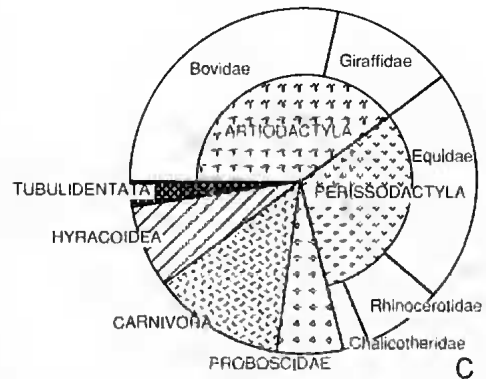
Hippotragini indet.



A



B



C

PALEOENVIRONMENTAL RECONSTRUCTION

The community of vertebrates from Çalta reflects quite well the environment in which it lived; this environment seems to have been contrasted, juxtaposing different types of biotopes.

The pie-diagram of figure 1A gives the relative proportions (in terms of MNI) of the various groups present at Çalta. Systematic screening yielded a great number of micromammals, among which gerbils are dominant, thus pointing to an open environment. When only large mammals are considered (Fig. 1B), we may notice the abundance of carnivores, probably greater than in living assemblages. As in the late Miocene of Kemiklitepe A + B (Fig. 1C, Bonis *et al.* 1994), bovids are the dominant group among artiodactyls, but the latter are more diverse at Çalta, with the addition of a suid and a cervid, than at Kemiklitepe A + B. However, several groups which occur in the upper Miocene are

Fig. 1. — Mammalian faunal composition of Çalta and Kemiklitepe A + B localities based on the minimum number of individuals. A, Çalta mammalian fauna with all groups; B, the same fauna without small mammals; C, Kemiklitepe A + B fauna without rodents.

missing at Çalta; some of them (Tubulidentata, Hyracoidea, Chalicotheriidae) may have become extinct in the meantime, but proboscideans sur-

vived in the area until the Pleistocene, and their absence here might have an ecological meaning. We may also, once more, notice the lack of cercopithecoid primates, a group which remains completely unknown in Turkey.

FUNCTIONAL ADAPTATIONS

One of the characteristics of this fauna is the marked lengthening of the distal segment of limb bones in several herbivores. This lengthening is an adaptation to running and implies therefore the presence of open landscapes. Thus *Hipparion* cf. *longipes*, as its name indicates, is characterized by lengthened limbs (Eisenmann & Sondaar this volume); *Gazella emilti* has limb bones longer than those of extant gazelles, and this is also the case of the Hippotragini (Bouvrain this volume). *Dicerorhinus megarhinus* is also a cursorial rhino (Guérin & Sen this volume). The Çalta giraffe is close to the African Plio-Pleistocene *Giraffa jumae*, which allows us to envisage a similar biotope to that of the living giraffe (Geraads this volume). This is also the case for the Çalta ostrich (Janoo & Sen this volume).

However, beside these herbivores with lengthened limb bones, there exist two taxa showing a different adaptation: *Tchaltacerus* is a small antelope with short and robust metapodials; such metapodials are currently known in bovids living in steep landscapes such as caprines (Bouvrain this volume). The strong shortening of the metacarpal bones in *Hipparion heintzi* as compared to the radius is found only in mountain zebras; however the widening of the hoofs in *Hipparion heintzi* contradict an adaptation to a steep landscape and would rather imply the presence of soft ground (Eisenmann & Sondaar this volume). The presence of an ochotonid also indicates the presence of mountain meadows and rocky grounds (Sen this volume).

Another characteristic of the Çalta vertebrate fauna is the great number of animals having a burrowing mode of life or even living underground. It is the case of several amphibians and reptiles; *Pelobates*, *Eryx*, amphisbaenians and scolecophidians (Rage & Sen 1976), but also of some rodents such as the Spalacidae and even the Gerbillidae that dig shallow but labyrinthine

burrows (Sen this volume). The pig *Sus arvernensis minor* is also known as a inhabitant of humid and hot loose soils in which it looks for its food (Guérin *et al.* this volume).

Two groups clearly indicate the presence of water bodies: frogs, although they are not very abundant, and an aquatic shrew, *Asoriculus*, which represents 64.9% of the insectivore remains (Reumer this volume). The presence of some murids (Sen this volume) and a deer (Geraads this volume) evidences the existence of a zone with abundant vegetation cover in the area.

The landscape of Çalta, when the fossiliferous deposits accumulated, seems to be mainly composed of steppic environments (cursorial animals, strong percentage of gerbils, spalacids and ochotonids, Sen this volume), with some water sources (persistent or temporary?), forested zones and also probably with some relief. Such an environment is in agreement with sedimentological results (Lunkka *et al.* this volume).

The climate could have been dry. Indeed the weak specific diversity of Soricidae would imply a dry and even arid climate (Reumer this volume). The specialization of the nasal region of *Hipparion heintzi* recalls the disposition existing in the Saïga antelope or in Camelidae and would mean an adaptation to an arid climate (Eisenmann & Sondaar this volume). Isotopic analyses show on the one hand the absence of C4 rich plants, therefore similar to the present day situation in central Anatolia, and on the other hand a strong evapotranspiration of plants corresponding to an open environment with arid conditions (Bocherens & Sen this volume).

Independently of indications provided by each taxon, one can try to draw conclusions from the global analysis of the Çalta mammalian community. From the various possible approaches, we have retained the method of the cenograms and the factor analysis of the taxonomic composition.

CENOGRAM

The cenogram (Valverde 1964; Legendre 1986) is a graph established by plotting the species on the X-axis in order of decreasing weight against the natural logarithm of their weight (in grams) on the Y-axis. The slope of the line(s) joining the points that correspond to the weight of each

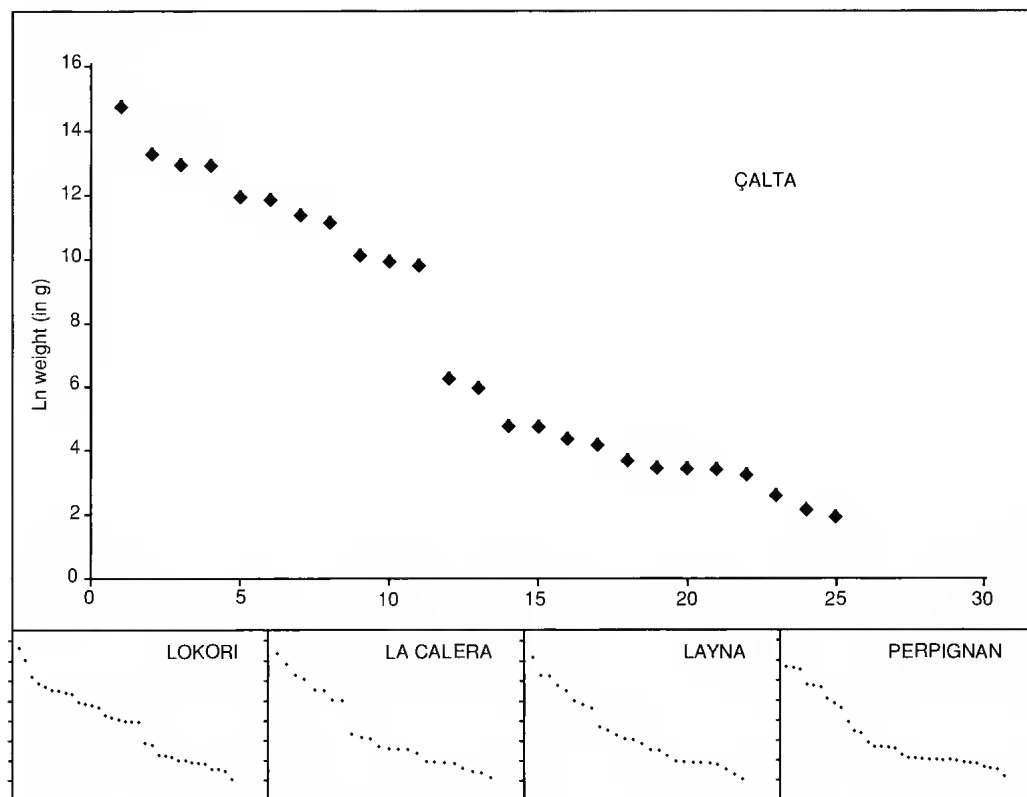


FIG. 2. — Cenogram of the Çalta mammalian fauna, compared with those of Lokori (present day dry woodland of Kenya), and of three Pliocene sites of western Europe. The data for the western European Pliocene sites is taken from Montuire (1994). The X and Y axes scales given for the Çalta cenogram are also used for the others.

taxon and the presence of possible breaks along this line(s) provide, according to these authors, indications on the humidity of the environment, its degree of openness, and even a minimal temperature estimation. We believe, however, that these graphs must be interpreted with caution, because the slope of the curve depends first on the number of species, therefore on the importance of excavations, and second on the graphic scale used. The most noticeable feature of the Çalta cenogram (Fig. 2) is the wide gap between larger (more than 18 kg) and smaller (less than 0.5 kg) species. This would suggest an open environment, much more open than those of the roughly contemporaneous sites of Layna (MN15, Spain) and Perpignan (MN15, France), and probably slightly more open than that of the extant Lokori fauna in Kenya which is from an

open forest/wooded grassland environment with a subarid climate. On the Çalta cenogram, the slope of larger mammals is not much steeper than that of smaller ones, implying that the climate was not very arid, less so than, *e.g.*, that of La Calera (MN14, Spain). The cenograms of the Spanish and French sites mentioned above are taken from Montuire (1994).

TAXONOMIC COMPOSITION

Mammalian communities also differ by their taxonomic composition, since the main mammalian groups are more or less abundantly represented depending on environmental factors. Multivariate analyses allow a better estimation of these differences. We have thus undertaken a factor analysis on twenty extant communities of the Ancient World (Table 1), by using as variables

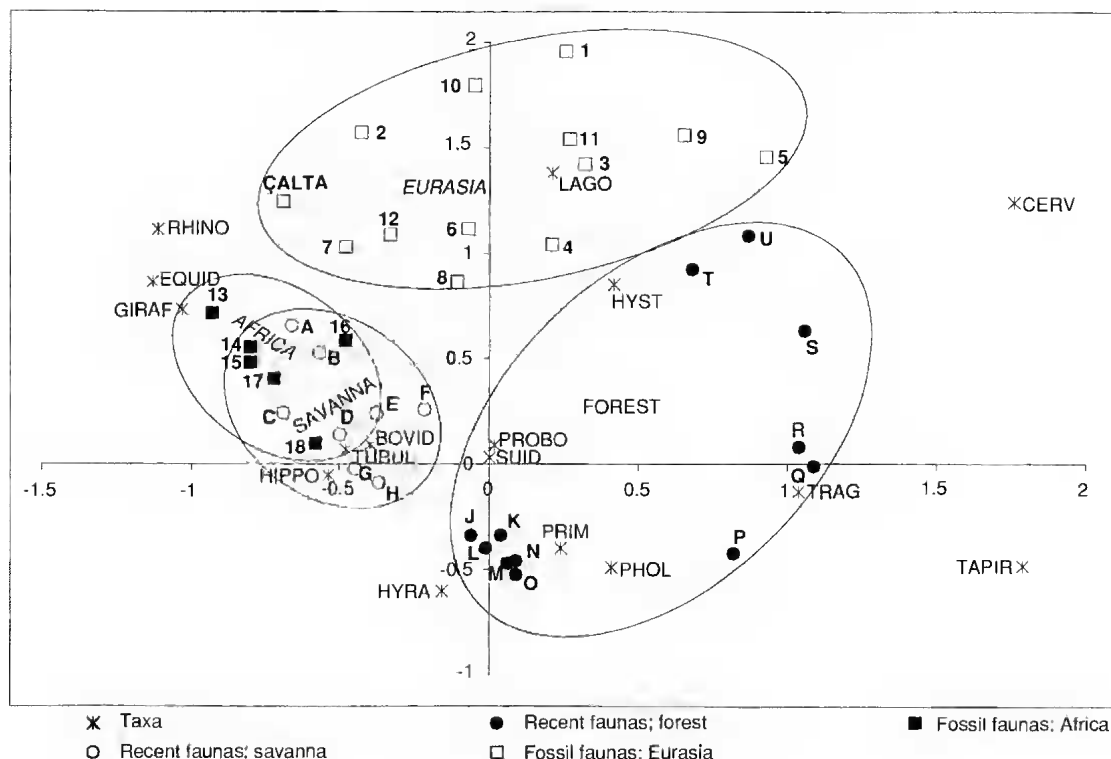


Fig. 3. — Correspondance factor analysis of Recent and Pliocene mammalian faunas. Matrix from references cited in tables 1, 2.

TABLE 1. — List of the sites with living mammalian communities used for factor analysis. Their environments and the related references are also given.

Sites	Countries	Environment	References
Umfoloji	A South Africa	savanna with acacias, gallery forest	Mentis 1970
Hluhluwe	B South Africa	deciduous humid forest	Bourquin <i>et al.</i> 1971
Chobe	C Botswana	flood plain	Sheppe & Haas 1976
Kafue	D Zambia	flood plain	Sheppe & Osborne 1971
Baoulé	E Mali	dry savanna	Bousquet 1992
Lomto savanna	F Ivory Coast	savanna with acacias, gallery forest	Bourlière <i>et al.</i> 1974
Niokolo-Koba	G Sénégal	wooded savanna, flood plain	Bousquet 1992
La Comoé	H Ivory Coast	wooded savanna, flood plain, forest	Lartigues & Poilecot 1997
Azagny	J Ivory Coast	marsh and forest	Bousquet 1992
Taï	K Ivory Coast	evergreen tropical forest	Bousquet 1992
Lamto forest	L Ivory Coast	montane forest	Bourlière <i>et al.</i> 1974
Makokou	M Gabon	equatorial forest	Happold 1996
Irangi	N Congo	equatorial forest	Rahm 1996
Mount Kivu	O Former Zaïre	montane forest, savanna, marsh	Rahm & Christiaensen 1963
Gunong Benom	P Malaysia	tropical rain forest	Medway 1972
Kuala Lompat	Q Malaysia	tropical rain forest	Medway & Wells 1971
Gunong Mulu	R Malaysia	tropical rain forest	Anderson <i>et al.</i> 1982
Wilpattu	S Sri Lanka	forest, flood plain	Eisenberg & Lockhart 1972
Gir	T India	open forest	Bernick 1974
Kanha	U India	forest, meadow	Schaller 1967

TABLE 2. — List, age and references of Pliocene localities used for factor analysis.

Localities		Countries	Age	References
Layna	1	Spain	MN15	Perez & Soria 1989-1990
La Calera	2	Spain	MN14	Alcala 1994
Villaroya	3	Spain	MN16	Azanza <i>et al.</i> 1989
Serrat-d'en-Vacquer	4	France	MN15	Mein 1990
Les Étouaires	5	France	MN16	Heintz <i>et al.</i> 1974
Dorkovo	6	Bulgaria	MN14	Thomas <i>et al.</i> 1986
Malusteni	7	Romania	MN15	Macarovici 1974
Kvabebi	8	Georgia	MN16	Vekua 1972
Karbolija	9	Moldavia	MN14/15	Pevzner <i>et al.</i> 1996
Yushe (Upper Gaozhuang)	10	China	MN15	Tedford <i>et al.</i> 1991, Fejfar <i>et al.</i> 1997
Çalta	ÇALTA	Turkey	MN15	this volume
Dinar-Akçaköy	11	Turkey	MN14	Van der Meulen & Kolfshoten 1986
Gülyazi	12	Turkey	MN16	Sickenberg <i>et al.</i> 1975
Warwire	13	Uganda	3.5 Ma	Pickford & Senut 1994
Nkondo	14	Uganda	4.5 Ma	Pickford & Senut 1994
KT 13	15	Tchad	3-3.5 Ma	Brunet <i>et al.</i> 1997
Laetoli	16	Tanzania	3.5 Ma	Harris <i>et al.</i> 1989
Tulu Bor	17	Kenya	3.5 Ma	Feibel <i>et al.</i> 1991
Lokochot	18	Kenya	3.5 Ma	Feibel <i>et al.</i> 1991

the main groups: Primata (PRIM), Lagomorpha (LAGO), Tubulidentata (TUBUL), Proboscidea (PROBO), Hyracoidea ((HYRA), Tapiridae (TAPIR), Rhinocerotidae (RHINO), Equidae (EQUID), Suidae (SUID), Hippopotamidae (HIPPO), Cervidae (CERV), Giraffidae (GIRAF) and Bovidae (BOVID). We have therefore excluded carnivores (that yield little ecological information, and whose number depends on the type of deposits), as well as bats and rodents (except Hystriidae: HYST) whose abundance also depends on taphonomic conditions. This analysis distinguishes well (plane 1-2, the CFA, Fig. 3) open habitats from closed ones (axis 1 especially), and also African faunas from those of Eurasia. If we replace on the same graph (as supplementary or illustrative elements) a set of faunas from the Pliocene of the Old World (Table 2), one can make several observations. As previously noticed by de Bonis *et al.* (1994), fossil faunas are systematically shifted in relation to the living ones. The distinction between African and Eurasian faunas nevertheless remains clear, since they are clearly separated in two different parts of this diagram. One can therefore rightfully think that the observations on the spatial distribution of extant faunas should be applied to fossil ones, and that it is therefore

possible to deduce some paleoecological conclusions from their comparison. African faunas would thus illustrate less varied habitats than Eurasian faunas, since they are more grouped and indicate in general more open environments. This corresponds well with what is known about them. One can then interpret the position of Çalta, on the very left of the graph, as reflecting a more open habitat than any other Eurasian locality. This result, even if it does not have to be accepted without nuances, corresponds well to indications provided by others approaches.

BIOGEOGRAPHY

The Çalta fauna is composed of three species of amphibians, ten reptiles, one bird and thirty-one species of mammals. This number clearly shows that this association is rich enough to be representative of the terrestrial faunal spectrum of the area during the time of deposition of the fossiliferous horizon.

Taken one by one, the genera and species recognized at Çalta have different affinities when compared to the geographic distribution of related groups. We will classify them in four categories, having in mind the affinity of each taxon, as

European, Eurasiatic, African and local. However, as we will see below, some taxa found at Çalta cannot be clearly related to a biogeographic province. For instance, *Giraffa* may appear as an African element of this fauna because of the past and present dispersal of all representatives of the genus, from the latest Miocene to Present; however, it may be considered as an Eurasian form if we take into account its phylogenetic relationships with the genus *Bohlinia* (late Miocene, Greece, Iraq).

EUROPEAN AFFINITIES

Among the Çalta mammals, the taxa having European affinities are dominant. The insectivores *Asoriculus gibberodon* and *Mafia csarnotense* are the common elements of central European Pliocene faunas (Reumer this volume). *A. gibberodon* was also found in the localities of Maramena, Maritsa and Tourkobounia-1 and, *M. csarnotense* at Apolakkia (Greece). These two species are not known in western and eastern Europe. The European rodents of Çalta are *Centralomys*, *Occitanomys*, *Dryomimus* and *Mimomys davakosi*. The species included in *Centralomys* were described from Italy, Greece and Turkey, and this genus has phylogenetic relationships with the western European *Castillomys*, and perhaps with *Occitanomys* (see Martin Suarez & Mein 1991). *Occitanomys* is a well-known western European genus, but de Bruijn (1976) and Black *et al.* (1980) referred to it, with a question mark, a new species from Turolian localities in Greece. Moreover, Storch (1987) included in this genus the doubtful "*Stephanomys*?" *pusillus* Schaub, 1938 from some latest Miocene localities in Inner Mongolia. If this attribution is correct, *Occitanomys* might have an Eurasian distribution, at least during the late Miocene. *Dryomimus* is apparently derived from the western European *Peridyromys* or *Myomimus* (Daams 1981). It occurs during the Pliocene in central and southeastern Europe. *Mimomys davakosi* is one of the oldest species referred to this genus, and it was found in localities close in age to the MN14/MN15 boundary in Greece, France and Spain. Although Radulescu & Samson (1989) suggested its synonymy with *Mimomys moldaviensis* Kormos, 1932 from Malusteni in Romania,

Fejfar *et al.* (1990) and Bachelet (1990) maintained it as a distinct species. Later representatives of the genus *Mimomys* are the common elements of the late Pliocene and early Pleistocene faunas all over Eurasia.

The Çalta rhino *Dicerorhinus megarhinus* is also exclusively European. It was discovered in almost all countries from Spain to Ukraine and Georgia during the Ruscinian (Guérin & Sen this volume). The geographic distribution of *Sus arvernensis* closely follows that of this rhino (Guérin *et al.* this volume).

The large overall size, the robustness, and even the upper cheek tooth morphology are rather similar in *Hipparion heintzi* from Çalta and in *H. crassum* (Eisenmann & Sondaar this volume). The latter species, the type locality of which is Perpignan in southern France, was also found in Greece.

An indeterminate bovid from Çalta can only be compared with *Koufotragus bailloudi* from the late Ruscinian of northern Greece.

ASIATIC OR EURASIATIC AFFINITIES

Among the Çalta mammals several groups have a wide geographic distribution across Eurasia. This is the case of *Erinaceus* sp. and *Apodemus dominans* which are known in many localities in Eurasia. *Orientalomys* is a murid which probably originated from Asia, but also occurred in southeastern Europe and Anatolia. *Pseudomeryx* has a similar distribution; it was found in China, Turkmenistan, Afghanistan, Turkey and Greece (see Sen this volume); it was also recorded in the Czech Republic with one tooth, and with one other tooth in Spain! Because of the lack of data on the phylogenetic relationships of this genus, it is not possible to recognize from where it originated.

The only lagomorph from Çalta is a new taxon, *Ochotonoma anatolica*, which is related to ochotonid genera *Proochotona*, *Pliolagomys*, *Ochotonoides* and *Ochotona*. This group has a long history and a wide distribution in Asia and eastern Europe; exceptionally its representatives emigrated to central and western Europe during the Pliocene and Pleistocene. This group is probably derived from the early-middle Miocene *Bellatona* which is well-known in central and eastern Asia.

Vulpes galaticus from Çalta is the oldest representative of the genus. Late Pliocene and early Pleistocene occurrences of *Vulpes* were mentioned all over Eurasia and North Africa. However, the attribution of several findings from Europe and Asia to the genus *Vulpes* is doubtful, for instance *Vulpes odessanus* from the Odessa-Catacombs, and inversely some other records described as *Canis* or *Nyctereutes* might well refer to *Vulpes*. The other carnivore *Lynx issiodorensis* has a geographic distribution covering all Mediterranean Europe, the Black Sea coastal areas and North Africa. The genera *Nyctereutes*, *Chasmaporthetes* and *Machairodus* have a wide geographic distribution from Spain to China and to Africa. Although all Çalta carnivores have their relatives in some North African Plio-Pleistocene localities, they are considered as having originated from Eurasia or even North America (Canidae) and they immigrated to Africa during the Pliocene.

Hipparion cf. *longipes* is represented at Çalta by ten postcranial bones, and is thus rarer than the other species *H. heintzi* (Eisenmann & Sondaar this volume). *H. longipes* is only known from the latest Miocene localities of Pavlodar and Kalmakpai in Kazakhstan. However, some related forms, similar in the proportions of limb bones but slightly smaller, have been found in the localities of Karaburun in Greece, Layna and La Gloria 4 in Spain.

Gazella emilii from Çalta is clearly different from the European Pliocene species *G. borbonica*, but quite similar to some species reported from central Asia (Bouvain this volume). The new genus and species *Tchaltacerus longicornis* is a Caprinae having resemblances with some species included in *Protorjyx* from Spain and Georgia. It is in any case related to the Eurasiatic goat-like bovids.

Some scarce remains of a Çalta bovid were determined as ? *Gazellospira* sp. This genus has a wide distribution from Spain to China.

AFRICAN AFFINITIES

Taxa with African affinities are rare at Çalta. Moreover, if even their living relatives are exclusively African, they did not necessarily originate from this continent. This is the case of the ostrich *Struthio* which is recorded in many Asian and

eastern European localities during the Miocene and Pliocene, while the extant distribution of this genus is limited to Africa. The same is also true for *Giraffa* sp. cf. *G. jumae*. Giraffids are well-known during the middle and late Miocene all over Eurasia and North Africa, but become rare during the Pliocene. The genus *Giraffa* first appears in East and South Africa around the Mio-Pliocene boundary, and it is quite well-represented in the Plio-Pleistocene East African faunas. However, this genus is probably derived from *Bohlinia* which is only known in late Miocene localities in Greece and Iraq. The Çalta giraffe cannot be the ancestor of its African relatives since this genus occurs earlier in Africa. However, it cannot be fully considered as of African origin because of the phylogenetic link between this genus and *Bohlinia*. Thus the Çalta giraffe might be either of eastern European or African origin, and we think it would be unwise to draw any biogeographic conclusion from it.

The remains of Hippotragini are quite rare at Çalta. It is apparently the unique element of this fauna which originated from Africa, since the Hippotragini first appears in East Africa during the late Miocene and later in Europe (Kvabebi, Georgia) and in the Siwaliks of Pakistan during the late Pliocene, about 2-3 Ma ago.

Pickford & Morales (1994) demonstrated that the enrichment of African elements in Spanish Neogene faunas is closely related to climatic fluctuations, itself regulated by the northern extension of the Ethiopian biogeographic realm. According to their results, the peaks of faunal change, which correspond to the maximum extension of the Ethiopian biogeographic realm, occurred at about 7 ± 0.5 Ma and 2.5 ± 0.5 Ma. The rarity of African elements in the Çalta fauna may be explained by the fact that it belongs to an intermediate phase between these dates. Nevertheless, the Pliocene faunas from the eastern Mediterranean regions are still poorly known to document enough the phase of African influences in mammalian communities.

LOCAL FORMS

Two rodent genera from Çalta, *Mesocricetus* and *Pliospalax*, are local forms. Their past and present distribution does not exceed the regions surround-

ding Turkey, i.e. from the Balkans to Iran and the Middle East.

In summary, the Çalta fauna is mainly composed of elements with European affinities, together with some forms that are clearly related to Asiatic groups. Species with African affinities are rare and their biogeographic relations are doubtful.

BIOCHRONOLOGY

The Çalta mammal locality is in fluvial deposits which do not contain any volcanic or volcanoclastic intercalations. Thus, it is not possible to apply radiometric dating techniques. In 1994 and 1995, J. Kappelman, J. P. Lunkka, D. Ekart and S. Sen sampled a 195 m thick section across the fossiliferous horizon for a magnetostratigraphic study. Paleomagnetic analyses of samples have been performed by J. Kappelman in the University of Texas at Austin. Unfortunately, it appeared that most samples are remagnetized probably because of tectonic tilting of deposits after deposition.

The Çalta section is not stratigraphically correlated to other mammal localities of the basin. Moreover, the nearest mammal localities Kavakdere and Çoban Pinar yielded Turolian mammal faunas, and thus they do not contain even one taxon in common with Çalta.

In Turkey, several Pliocene mammal localities are already known. However, most of them have preliminary faunal lists, and the others are low in species diversity. So, unfortunately, they are not reliable for detailed biochronologic comparisons. In Greece, Pliocene mammal faunas are better known from a dozen localities (Van der Meulen & Kolfschoten 1986; Koufos & Kostopoulos 1997). Thanks to faunal lists published by these authors and the studies mentioned therein, the Çalta fauna can be compared with some of them. In addition, the close biogeographic affinities of this fauna with those from Eurasia also provides biochronologic criteria for correlation.

Figure 4 shows the biochronologic distribution of some selected genera and species from Çalta. Most of them appear during the late Turolian or early Ruscinian, and they have a time range generally covering the entire Pliocene. However,

some of them are more restricted in time and can be used as key elements to date this fauna. This is the case of the insectivore *Mafia csarnotense*; its oldest known occurrence is at Podlesice (late MN14, Poland), and the youngest one at Csarnota-2 (late MN15, Hungary). This species was also found in Apolakkia (late MN15, Greece). Moreover, studying the Çalta insectivores, Reumer (this volume) noted the absence of Crocidurinae in this fauna as a proof of its earlier age in comparison to localities where this group exists. Crocidures originated from Africa; their earliest occurrence in Europe is in the locality of Apolakkia, Rhodes Island, Greece (Weerd *et al.* 1982; Reumer 1984). This locality is dated as late MN15. Later on this group becomes common in Villanyian and younger faunas in Europe.

Pseudomeriones is a gerbil which occurs from the latest Vallesian to ? middle Villafranchian in China, Turkmenistan, Afghanistan, Greece and Turkey. In the Aegean area, its representatives are *P. cf. abbreviatus* in latest Vallesian and Turolian localities, *P. rhodius* at Ano Metchi (MN13) and Maritsa (MN14) and *P. tschaltaensis* at Çalta. The latter species is more derived than the others (Sen this volume), which favours an age younger than Maritsa.

Mimomys davakosi was only reported from the early MN15 faunas: Ptolemais 3 (type locality, Greece) and Serrat-d'en-Vacquer (reference locality of MN15, southern France). It is considered as one of the oldest and most primitive species of the genus. The great agreement among the rodent specialists is that the appearance of *Mimomys* defines the base of MN15. The other primitive species of *Mimomys* is *M. antiquus* from Peshniov-Borki and Borehole No. 2 along the River Ob in western Siberia (Zazhigin 1980), both localities dated as MN15a (Fejfar *et al.* 1997). Radulesco & Samson (1989) suggested the synonymy of *M. davakosi* with another primitive *Mimomys* from Malusteni (MN15a, Romania), *M. moldavicus* Kormos, 1930. Fejfar *et al.* (1990, 1997) retained this opinion with some caution because of the poor state of preservation of the Malusteni specimens. *M. vandermeuleni* Fejfar *et al.*, 1990 from Spanish localities is also characterized by low dental tracts, strong

	VALLESIAN		TUROLIAN			RUSCINIAN		VILLANYIAN		EI PLEISTOCENE													
MN zones Genera	MN9	MN10	MN11	MN12	MN13	MN14	MN15	MN16	MN17														
<i>Asoriculus</i>																							
<i>Mafia</i>																							
<i>Apodemus</i>																							
<i>Orientalomys</i>																							
<i>Centralomys</i>																							
<i>Mesocricetus</i>																							
<i>Pseudoniviones</i>																							
<i>Mimomys</i>																							
<i>Dryomimus</i>																							
<i>Vulpes</i>																							
<i>Nyctereutes</i>																							
<i>Chasmaporthetes</i>																							
<i>Lynx</i>																							
<i>Macrairodus</i>																							
<i>H. longipes</i> -type																							
<i>H. crassum</i> -type																							
<i>Dicerorhinus</i>																							
<i>megarhinus</i>																							
<i>Sus arvernensis</i>																							
<i>Giraffa</i>																							
	Sinap Loc.8A	Bayraktepe II	Kaleköy Karabzu	Kayadibi	Kemiklitepe D	Kemiklitepe A+B	Samos Q1	Dytko	Maramena Aro Melochi	D. Akcakoy Develli Maritsa	D. Akcakoy Develli Maritsa	ÇALTA	Apollonia-1	Gerakarov	Daimero Woaks	Gulyazi	Toukrobouna-1	Megalo Emvolon	Apollakia	ÇALTA	Gerakarov	Apollonia-1	LOCALITIES

FIG. 4. — Stratigraphic distribution of some genera and species represented in the Çalta fauna.

roots and an occlusal pattern similar to that of *M. davakosi*. Some Spanish localities yielding this species were dated by magnetostratigraphy as about 4 Ma old, and the others correlated to early MN15 (Opdyke *et al.* 1997; Fejfar *et al.* 1997). In Spain as well as in other parts of Europe, late MN15 and later faunas include *Mimomys* species with a more derived dental pattern: higher dentine tracts, roots smaller, increase of the hypsodonty, appearance of *Dolomys*-pattern, etc. This review shows that the Çalta *Mimomys* remains among the earliest known species of this genus.

Taking into account the bulk of the Çalta fauna, and more particularly the time range and the

stage of evolution of some key taxa, it seems obvious that this fauna should be dated as MN15, and more probably in the lower part of this zone.

In the Teruel Basin in eastern Spain, Opdyke *et al.* (1997) studied the magnetic stratigraphy of several sections bearing Turolian, Ruscian and Villanyian mammal localities. Using magnetostratigraphic correlations from the Orrios, Villalba Alta, Escoribuela and Loma del Castillo sections, they calibrated the MN14/MN15 boundary as 4.18 Ma, and the MN15/MN16 boundary as correlative to Gilbert/Gauss boundary at 3.58 Ma. They also obtained boundary ages for older (Turolian) and younger

(Villanyian) MN zones which are out of the scope of the present study. On the other hand, magnetostratigraphy of Pliocene mammal localities in Romania calibrated the Dacian/Romanian boundary at about 4.2 Ma (Sen 1997); this boundary is considered as equivalent to the MN14/MN15 boundary of the European mammalian zonation. These results agree in the attribution of an age about 4 Ma to the Çalta fauna.

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